

The coralliophiline (Gastropoda: Muricidae) radiation: repeated colonizations of the deep sea?

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ABSTRACT

The Coralliophilinae are a subfamily of Muricidae, with about 200–250 species, mostly from temperate and tropical oceans, that are associated with anthozoans on which they feed. We present here a phylogenetic hypothesis for the subfamily, based on DNA sequences (650 aligned positions) of the mitochondrial 12S rDNA from 42 coralliophilines and six other muricids, as well as one fascioliid, which serves as the outgroup. Relationships among the muricid subfamilies were not resolved unequivocally, but coralliophiline monophyly was strongly supported. Two major clades emerged within the Coralliophilinae, both well supported in a Bayesian analysis. The genera *Coralliophila* and *Babelomurex* as commonly understood, are clearly polyphyletic, and in need of redefinition. Our results indicate multiple, independent incursions of Coralliophilinae into deep water habitats, several producing subsequent radiations.

Additional keywords: Neogastropoda, Coralliophilinae, *Coralliophila*, *Babelomurex*, 12s rDNA

INTRODUCTION

Coralliophila and related genera (e.g., *Babelomurex*, *Latiaxis*, *Leptoconchus*, and *Quoyula*) comprise the muricid subfamily Coralliophilinae, a highly diverse lineage of neogastropods that contains approximately 200–250 described species distributed worldwide, mostly in warm temperate and tropical oceans. These species are traditionally partitioned among 7–10 genera based on shell morphology. The known fossil record for coralliophilines extends to at least the middle Eocene (circa 40 Ma). All species for which the ecology is known are symbionts (ecto or endobiotic) of anthozoans (including sea-anemones, gorgonians and reef-building coral species), on which they feed.

The Coralliophilinae are well represented in deep water faunas of the tropical and subtropical Atlantic and Indo-Pacific oceans. Deep habitats are those in excess of 100–150 m, which is the depth limit for hermatypic scleractinians. Beyond these depths, they are replaced by Alcyonaria, Stylasterina and Porifera. In temperate regions, these depth limits are likely to be closer to the surface, in the range of 50–100 m (mostly dependant on the turbidity of the water), where marine phanerogams and green algae (along with the non hermatypic zooxanthellate hexacorals) are progressively replaced by sponges, red algae, and octocorals.

A detailed, quantitative analysis of shallow and deep faunas by area has not yet been conducted. However, even a conservative approach (i.e., extrapolating the "tropical" bathymetric boundary of 100–150 m to all regions) reveals a high proportion of deep-water species within Coralliophilinae, ranging between 65–80% for most regions, with a global average of 75% (Oliverio, 2008a, 2008b, In press; Marshall and Oliverio, In press; M. Oliverio and C. Smriglio, pers. observ.)

In the absence of a detailed fossil record of the Coralliophilinae, it is unclear whether the group originated in shallow water, with subsequent colonizations of deep water habitats, or if the ancestral members of the subfamily evolved in deeper waters, with subsequent invasions of photic habitats. A phylogenetic framework would aid in distinguishing between these mutually exclusive evolutionary scenarios.

Previous studies based on the morphology of digestive and reproductive systems, along with data on developmental and alimentary ecology (Richter and Luque, 2002), indicated monophyly of coralliophilines, with significant differences from the muricid *bauplan*, suggesting a derived, monophyletic radiation from an early muricoid ancestor. Preliminary molecular phylogenetic studies (Oliverio and Mariottini, 2001; Oliverio et al., 2002),

despite limited taxonomical coverage (11 species, ~5% of the known species), clearly showed that coralliophilines originated within the muricid radiation, indicating a probable sister group relationship with the rapanina lineage(s).

We present herein a phylogenetic study based on partial sequence of the 12S rDNA (a portion corresponding to domain III), performed on 35 coralliophiline species (i.e., circa 15% of their known species diversity) and seven outgroup taxa. The goal of this study is to uncover the relationships of the Coralliophilinae within the family Muricidae, and of as many genera as possible within the subfamily.

MATERIALS AND METHODS

TAXON SAMPLING AND SPECIMEN COLLECTION: A total of 41 sequences were analyzed in this study. Of these, 12 were derived from previous works (Oliverio and Mariottini, 2001; Oliverio et al., 2002; Mariottini et al., 2005). Thirty new sequences were determined with the goal of enlarging the taxonomic coverage to include as much of the morphological diversity of the Coralliophilinae as possible. Taxon names, locality data, voucher information, and EMBL (The European Molecular Biology Laboratory, Heidelberg) accession numbers are provided in Table 1. *Fasciolaria liguaria* (Fasciariidae) was selected to serve as the outgroup for our sequence analyses. Voucher specimens of most samples are stored at Muséum national d'Histoire naturelle (MNHN, Paris) and at Dipartimento di Biologia Animale e dell'Uomo (DBAU, Rome). Double ID in Table 1 indicates that the primary voucher is stored at MNHN and tissue samples of the voucher and/or specimen(s) from the same lot are stored at DBAU.

Sequences from six muricids, representing five additional subfamilies were included in our analyses in order to reassess the monophyly of Coralliophilinae, and the sister group relationship with the Rapaninae that was previously hypothesized by Oliverio and Mariottini (2001).

DNA EXTRACTION, PCR, CLONING AND SEQUENCING: Total DNA was extracted following a standard Phenol/Chloroform/Ethanol protocol (Hillis et al., 1990) with slight modification as previously described by Oliverio and Mariottini (2001). DNA from difficult samples was extracted by the QIAGEN QiAmp Extraction Kit, according to manufacturer's instructions. DNA from formalin-fixed samples was extracted with the standard protocol after washing the tissue sample 3–5 times with PBS.

Partial sequences of the mitochondrial gene encoding the 12S ribosomal DNA were PCR amplified, with the primers *12SI* (5'-TCGCCAGCAGCCGCGGTTA-3') and *12SIII* (5'-GAGCGACGGCCGRTTWGTAC-3') (Oliverio and Mariottini 2001). Amplification conditions were as follows: 94°C for 30 seconds, 45–50°C for 30 seconds, 72°C for 60 seconds (30–35 cycles). The PCR products were purified using the Exo-Sap enzymatic method, and double strand sequenced using the PCR primers. Sequencing was performed by Macrogen Inc. (Seoul, Korea). Chromato-

grams were analysed by Staden Package (Version 1.6.0, Staden et al., 1998, 2005). All sequences have been deposited at EMBL (see Table 1 for accession numbers).

SEQUENCE AND PHYLOGENETIC ANALYSIS: The 12S sequences were aligned using the default settings in ClustalX (Thompson et al., 1997) and then manually edited. Sequence data were analyzed for their fit (AIC criterion) to different models of nucleotide substitution using Modeltest v. 3.7 (Posada and Crandall, 1998) and MrModeltest v. 2.2 (Nylander, 2004) with the package PAUP* v. 4.0b10 (Swofford, 2002).

Analysis of the nucleotide sequence was performed using Mega3.1 (Kumar et al., 2004). The uncorrected pairwise distances (p) and the ML distances (i.e., pairwise distances corrected by the assumed model of evolution estimated) between the sequences were calculated. To test for the presence of mutational saturation, uncorrected p distances, transition (Ts) and transversion (Tv) were plotted against the estimated ML distance (Nichols, 2005; Philippe et al., 1994). The aligned sequences were analyzed under the assumptions of maximum likelihood (ML: Felsenstein, 1981) and by Bayesian inferences (BI), using the packages Treefinder (Jobb, 2007) and MrBayes v. 3.1.2 (Ronquist and Huelsenbeck, 2003), respectively. Support to the nodes was calculated for ML trees by using the Expected-Likelihood Weights (ELW: Strimmer and Rambaut, 2002) and bootstrap (bs) for 1000 replicates, as computed in Treefinder. A Bayesian analysis (BI) was performed to obtain posterior probabilities of branches using the software MrBayes, which adopts the Markov Chain Monte Carlo method to sample from posterior densities (Larget and Simon, 1999; Yang and Rannala, 1997). The model of evolution was the one chosen by MrModeltest. A four chain metropolis-coupled Monte Carlo analysis was run twice in parallel for 1.5×10^6 generations, and trees were sampled every 100 generations, starting after a burn-in of 375,000 generations. Bayesian posterior probabilities (bpp) were estimated on a 50% majority rule consensus tree of the sampled trees (after burn-in).

RESULTS

Partial sequences of the 12S ribosomal rRNA genes were determined and analyzed to explore the phylogenetic relationships among coralliophilines representing 34 species in 7 genera. The resulting sequences ranged in length from 507 bp in *Coralliophila panormitana* (Monterosato, 1869) to 548 bp in *Hexaplex trunculus* (Linnaeus, 1758) excluding the primers. The multiple sequence alignment resulted in a total of 563 nucleotide positions, including gaps.

Modeltest and MrModeltest estimated the GTR+I+G model ($\alpha = 0.7948$; Pinvar = 0.2336) as the relatively best-fit model of nucleotide substitution for the dataset. The mutational saturation analysis (not shown) indicated that transitions started becoming saturated at a ML distance corresponding to inter-subfamilial comparisons.

Table 1. Species included in the molecular analysis, with voucher ID (BAU: Dept of Animal and Human Biology, Rome; MNHN, Muséum National d'Histoire Naturelle, Paris; NMSA: Natal Museum, Pietermaritzburg), collecting data, and EMBL accession numbers. OM2001 refers to Oliverio and Mariottini (2001), MSR2005 to Mariottini, Smriglio and Rolán (2005). If two IDs are given, the primary voucher is stored at MNHN (see text).

Family	Subfamily	Specimen ID	Locality	EMBL Accession Numbers	
				12S	Ref.
Muricidae					
Coralliophilinae	<i>Babelomurex amaliae</i> (Kobelt, 1907)	BAU00332	Astypalaya Is. (Greece) 36°33' N, 026°22' E, 35 m depth	AJ293671	OM2001
	<i>Babelomurex armatus</i> (Sowerby, 1912)	MNHN IM-2009-5110 BAU00333	Balicasag Is. (Philippines), tangle net. 9°30'50" N 123°41'16" E, 150 m depth.	FN391955	This work
	<i>Babelomurex cariniferus</i> (G. B. Sowerby II, 1834)	MNHN IM-2009-5111 BAU00334	Ustica Is. (Sicily, Italy), 10 m depth	FN391956	This work
	<i>Babelomurex bernardi</i> Nicolay, 1984	MNHN IM-2009-5112 BAU00335	C d'Ivoire, intertidal.	FN391957	This work
	<i>Babelomurex cristatus</i> (Kosuge, 1979)	MNHN IM-2009-5094 BAU00004	Panglao Is., Momo Beach (Philippines), PANGLAO 2004, st. P4, 9°36' N, 123°45' E, 80 m depth.	FN391958	This work
	<i>Babelomurex deburghiae</i> (Reeve, 1857)	MNHN IM-2009-5095 BAU00002	Bohol Island, Maribohoc Bay (Philippines), PANGLAO 2004, st. P1, 9°36' S, 123°45' E, 90–200 m depth.	FN391959	This work
	<i>Babelomurex diadema</i> (A. Adams, 1854)	MNHN IM-2009-5096 BAU00003	Bohol Island, Maribohoc Bay (Philippines), PANGLAO 2004, st. P1, 9°36' S, 123°45' E, 90–200 m depth.	FN391960	This work
	<i>Babelomurex gemunatus</i> (Shikama, 1966)	MNHN IM-2009-5097 BAU00013	Panglao Is., Momo Beach (Philippines), PANGLAO 2004, st. P4, 9°36' N, 123°45' E, 80 m depth.	FN391961	This work
	<i>Babelomurex lischkeanus</i> (Dunker, 1822)	MNHN IM-2009-5098 BAU00010	Nord Bellona (New Caledonia), EBISCO 2005, st. DW2578, 20°21' S, 158°40' E, 440–505 m depth.	FN391962	This work
	<i>Babelomurex nakayasui</i> (Shikama, 1970)	MNHN IM-2009-5099 BAU00005	Bohol Island, Maribohoc Bay (Philippines), PANGLAO 2004, st. P1, 9°36' S, 123°45' E, 90–200 m depth.	FN391963	This work
	<i>Babelomurex princeps</i> (Melville, 1912)	MNHN IM-2009-5100 BAU00355	Norfolk Ridge (New Caledonia), NORFOLK I, st. CP1713, 23°22' S, 168°02' E, 204–216 m depth.	FN391964	This work
	<i>Babelomurex spinosus</i> (Hirase, 1908)	MNHN IM-2009-5101 BAU00006	Banc Kelso (New Caledonia), EBISCO 2005, st. DW2520, 24°06' S, 159°41' E, 350–400 m depth.	FN391965	This work
	<i>Babelomurex yamatoensis</i> Kosuge, 1986	MNHN IM-2009-5102 BAU00011	Banc Nova nord (New Caledonia) EBISCO 2005, st. DW2533, 22°18' S, 159°28' E, 360 m depth.	FN391966	This work
	<i>Babelomurex yumimarumai</i> Kosuge, 1985	MNHN IM-2009-5103 BAU00336	Scorff passage (Vanuatu), SANTO 2006, st. EP12, 15°32' S, 167°15' E, 97 m depth.	FN391967	This work
	<i>Coralliophila brevis</i> (Blainville, 1832)	BAU00337	La Maddalena Is. (Sardinia, Italy), 41°15' N, 009°26' E, 30 m depth	AJ293676	OM2001
	<i>Coralliophila bulbiformis</i> (Conrad, 1837)	MNHN IM-2009-5104 BAU00012	Baldwin Bay (Vanuatu), SANTO 2006, st. FR58, 15°35' S, 167°02' E, 3–18 m depth	FN391968	This work

(Continued)

Table 1. (Continued.)

Family	Subfamily	Specimen ID	Locality	EMBL Accession Numbers	
				12S	Ref.
	<i>Coralliophila caribaea</i>	BAU00338	Juan Dolio, Santo Domingo, 15 m depth	AJ293677	OM2001
	<i>Coralliophila clathrata</i> (A. Adams, 1854)	BAU00339	Mtvalume, Natal (South Africa) intertidal rock pools (D. Herbert leg, 14.iii.1986)	FN391969	This work
	<i>Coralliophila costularis</i> (Lamarck, 1816)	MNHN IM-2009-5113 BAU00340	Darsa Is., N side, Soqatra Archipelago (Yemen), 7 m depth, 9.ii.2000	FN391970	This work
	<i>Coralliophila crosa</i> (Röding, 1798)	MNHN IM-2009-5105 BAU00341	East Malo Island (Vanuatu), SANTO 2006, st. DBS6, 15°38'S, 167°15'E, 13 m depth	FN391971	This work
	<i>Coralliophila fontanangioyi</i> Smriglio and Mariottini, 2000	MNHN IM-2009-5114 BAU00342	Teno Sur, Tenerife, Canary Is. (Spain), 25°20'30" N 16°55'30" W, 15 m depth 20.11.94 on <i>Madracis asperula</i>	FN391972	This work
	<i>Coralliophila kaofitorum</i> Vega-Luz, Vega-Luz and Luque, 2002	MNHN IM-2009-5115 BAU00343	Teno Sur, Tenerife, Canary Is. (Spain), 25°20'30" N 16°55'30" W, 32 m depth 20.11.94 on <i>Antipates wollastoni</i>	FN391973	This work
	<i>Coralliophila meyendorffii</i> (Calcara, 1845)	BAU00344	Cape Circeo (Latium, Italy), 41°11' N, 013°04' E, 7 m depth	AJ297519	OM2001
	<i>Coralliophila violacea</i> (Kiener, 1836)	BAU00345	Taiwan, 23°10'N, 120°05'E 5 m depth	AJ293679	OM2001
	<i>Coralliophila panormitana</i> Monterosato, 1869	BAU00346	Cape Circeo (Latium, Italy), 41°11' N, 013°04' E, 70 m depth	AJ293681	OM2001
	<i>Coralliophila radula</i> (A. Adams, 1855)	BAU00015	Rarotonga (Cook Islands), 21°12'S 159°43'W, 12 m depth.	FN391974	This work
	<i>Coralliophila squamosissima</i> (E. A. Smith, 1876)	NMSA D9663	Boteler Point, Zululand (South Africa), 27°00'42" S 32°52'00" E, intertidal rock pools, amongst <i>Palythoa</i> sp. July 1987	FN391975	This work
	<i>Coralliophila trigoi</i> Mariottini, Smriglio, and Rolán, 2005	BAU00347	Camarinas, Galicia (Spain), northeastern Atlantic Ocean, 15–50 m depth	AJ937305	MSR2005
	<i>Hirtomurex filiaregis</i> (Kurohara, 1959)	MNHN IM-2009-5106 BAU00014	West Bellona (New Caledonia) EBISCO 2005 st. DW2549, 21°07' S, 158°38' E, 330 m depth.	FN391976	This work
	<i>Latiaxis hayashii</i> (Shikama, 1966)	MNHN IM-2009-5116 BAU00348	Norfolk Ridge, 23°45'S, 168°17'E, 400–500 m depth.	FN391977	This work
	<i>Latiaxis pilsbryi</i> Hirase, 1908	MNHN IM-2009-5107 BAU00008	Banc Nova north (New Caledonia) EBISCO 2005, st. DW2534, 22°17' S, 159°25' E, 390 m depth.	FN391978	This work
	<i>Leptoconchus</i> sp.	MNHN IM-2009-5108 BAU00062	Panglao Is., Sungcolan (Philippines), PANGLAO 2004, st. R47, 9°39' S, 123°49' E, 4–25 m depth.	FN391979	This work
	<i>Quoyula monodonta</i> (Sowerby, 1832)	BAU00349	Bunaken Is. (Sulawesi, Indonesia), 01°37'N, 124°46'E.	AJ293675	OM2001

(Continued)

Table 1. (Continued.)

Family	Subfamily	Specimen ID	Locality	EMBL Accession Numbers	
				12S	Ref.
	<i>Rapa rapa</i> (Linnaeus, 1758)	MNHN IM-2009-5109 BAU00085	Panglao Island, Napaling (Philippines), PANGLAO 2004, st. R19, 9°37' N, 123°46' E, 2–54 m depth.	FN391980	This work
Ocenebriinae	<i>Nucella lapillus</i> Linnaeus, 1758	BAU00187	Portobello (UK), 55°57' N 3°06' W, intertidal	AJ293668	OM2001
Muricinae	<i>Hexaplex trunculus</i> (Linnaeus, 1758)	BAU00351	San Pietro Is. (Sardinia, Italy), 39°09' N, 008°12' E, 3–4 m depth	AJ293669	OM2001
Muricopsinae	<i>Muricopsis cristata</i> (Brocchi, 1814)	MNHN IM-2009-5117 BAU00352	San Pietro Is. (Sardinia, Italy), 39°09' N, 008°12' E, 3–4 m depth	FN391981	This work
Rapaninae	<i>Cronia</i> sp.1	MNHN IM-2009-5118 BAU00619	Tolo Channel, Hong Kong, 22°27' N, 114°16' E, 1 m depth	FN391982	This work
	<i>Cronia</i> sp.2	MNHN IM-2009-5119 BAU00188	Rarotonga (Cook Islands), 21°12' S 159°43' W, 12 m	FN391983	This work
	<i>Stramonita haemastoma</i> (Linné, 1767)	BAU00354	San Pietro Is. (Sardinia, Italy), 39°09' N, 008°12' E, 3–4 m depth	AJ293670	OM2001
Fascioliariidae					
Fascioliariinae	<i>Fasciolaria lignaria</i> (Linnaeus, 1758)	BAU00350	San Pietro Is. (Sardinia, Italy), 39°09' N, 008°12' E, 3–4 m depth	AJ293682	OM2001

Figure 1 illustrates the tree recovered from the Bayesian analysis. As maximum likelihood ELW and bootstrap values (bs) were identical to four decimal places, only the bs are indicated on the tree, along with the bayesian posterior probabilities (bpp). Monophyly of Coralliophilinae was well supported in both ML (100 bs) and BI analyses (100 bpp). A sister-group relationship with the Rapaninae, represented in the tree by *Stramonita haemastoma*, did not receive high support, while BI supported a closer relationship of Coralliophilinae with Muricopsinae (represented by *Muricopsis cristata*) than with any other muricid.

The internal arrangement of the coralliophilines in the tree was characterized by the sorting of the species into two well-supported clades: Clade A (93 bpp) included *Quoyula monodonta*, *Babelomurex lischkeanus*, the endobiotic taxa (*Rapa*, *Leptoconchus*), and the Eastern Atlantic/Mediterranean species usually included in *Coralliophila*; Clade B (100 bpp, 100 bs) included the remaining *Coralliophila* species, along with the taxa traditionally ascribed to *Latiaxis*, *Hirtomurex*, and *Babelomurex*.

DISCUSSION

Coralliophilinae has been regarded (either explicitly or implicitly) as a monophyletic group since Thiele (1929), who erected the family Magilidae based on the absence of jaws or a radula. Subsequent workers suggested other characteristics (e.g., a long pleurembolic proboscis, absence of accessory salivary glands, absence of dorsal glandular folds of the oesophagus, and fusion of the paired salivary ducts into a single duct) as possible synapomorphies of Coralliophilinae (Gohar and Soliman, 1963; Ward, 1965; Ponder, 1973; Massin, 1987, 1990; Kantor, 1995). Our present molecular analysis, with a significant sampling of coralliophiline taxa for partial 12 S rDNA sequences, strongly supports the monophyly of Coralliophilinae (with high ELW, bootstrapped ML, and bpp), substantiating the preliminary conclusions from our previous studies (Oliverio and Mariottini, 2001; Oliverio et al., 2002).

Harasewych et al. (1997) as well as Oliverio and Mariottini (2001) and Oliverio et al. (2002), reported a sister group relationship between Coralliophilinae and Rapaninae. In the present study, we failed to recover this relationship. Instead, Muricopsinae and Ocenebriinae emerge as being more closely related to Coralliophilinae than did Rapaninae. However, given the level of saturation of transitions at maximum likelihood distances corresponding to inter-subfamilial comparisons, as well as the poor taxonomic sampling of muricid subfamilies, these results should be considered preliminary.

The results of the current analyses reveal that Coralliophilinae are resolved into two distinct clades (A and B in Figure 1), each with high levels of support, confirming the preliminary indications by Oliverio and Mariottini (2001) and Oliverio et al. (2002). Clade A includes *Quoyula monodonta*, *Coralliophila clathrata*, the endobiotic taxa (*Rapa*, *Leptoconchus*), the deep-water enigmatic taxon "*Babelomurex*" *lischkeanus*, and the Eastern

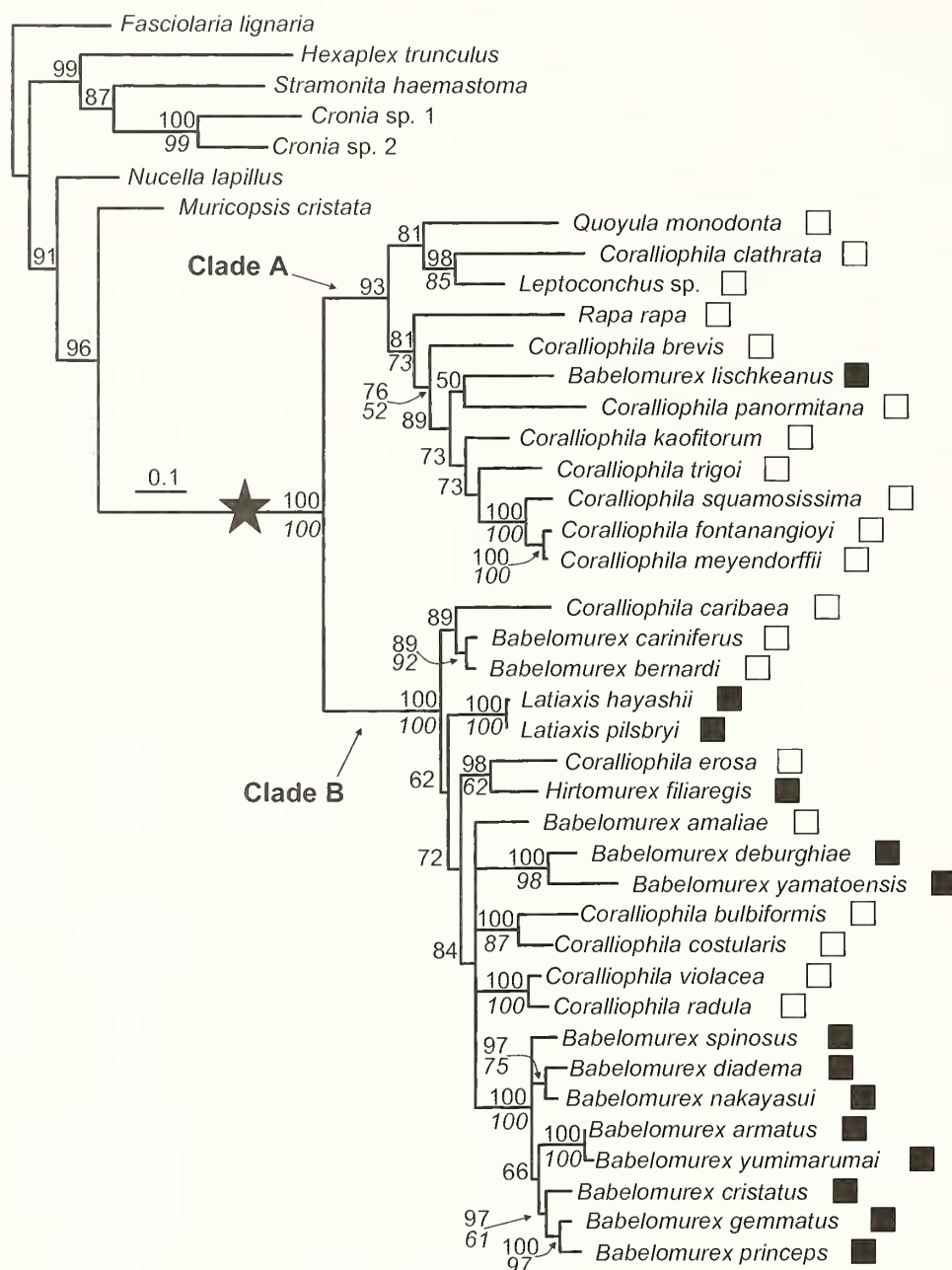


Figure 1. Bayesian tree, portraying phylogenetic relationships among the assayed species. Numbers at the node are Bayesian posterior probabilities (11,250 trees) and maximum likelihood bootstrap supports (1000 replicates; in *italic*). The star indicates the branch leading to the monophyletic Coralliophilinae. Symbols: ■, deep water species; □, shallow water species.

Atlantic/Mediterranean species usually included in *Coralliophila*. The positions of the endobiotic *Leptoconchus* sp. and *Rapa rapa* in the tree suggest that endobiosis may have originated at least twice in this group, a parsimonious hypothesis to be further tested. *Leptoconchus* species are endoparasites of Hexacorallia, while *Rapa* species live within soft corals (Octocorallia). *Quoyula monodonta* feeds upon Scleractinia and *Coralliophila clathrata* on Zoanthidea. We infer that this clade had its origins as ectoparasites of shallow water hexacorals, with

a single ascertained shift to octocorals (*Rapa*), two adaptations for endobiosis, and at least one colonization of deep water habitats (*"B."* *lischkeanus*).

Clade B includes all the remaining coralliophiline species in our study. The close, sister group relationship (100 bs, 100 bps) between *Latiaxis hayashii* and *L. pilsbryi* supports the monophyly of the genus *Latiaxis* sensu stricto (the type species, *L. mawae*, was not included in the analysis.) However, the monophyly of the widely used genera *Coralliophila* and *Babelomurex* are not supported.

Oliverio and Mariottini (2001) and Oliverio et al. (2002) suggested that the genus *Coralliophila*, as usually understood, may be polyphyletic. The type species of *Coralliophila*, *C. violacea*, forms a pair with the morphologically similar, Indo-Pacific *C. radula*, and, with another pair (*C. bulbiformis* and *C. costularis*), are included in a clade predominated by eleven species of *Babelomurex*. Two other species, the Caribbean *C. caribaea* and the Indo-Pacific *C. crosa*, belong in Clade B. Most of the species usually included in *Coralliophila* s.l. are in clade B. We urge the need for a re-definition of the genus *Coralliophila*, and for a restriction of its use. For the other species traditionally included in *Coralliophila* there is a long list of names, potential candidates for the other lineages (e.g., *Pseudomurex* Monterosato, 1872).

The type species of *Babelomurex*, the eastern Atlantic/Mediterranean *B. cariniferus*, emerges as the sister taxon of the West African *B. bernardi*, a relationship well supported by shell morphology. Both species live in shallow waters. Most of the remaining species assigned to the genus *Babelomurex* form a well defined clade (*B. spinosus*, *B. diadema*, *B. nakayasui*, *B. armatus*, *B. yuntinarumai*, *B. cristatus*, *B. gemmatus* and *B. princeps*), of deep-water Indo-Pacific species that do not appear to be monophyletic with the type species of *Babelomurex*. This group is likely the result of an independent radiation following the shift to a deep-water habitat by a shallow water ancestor. Other species of *Babelomurex*, *B. deburghiae*, *B. yamatocensis*, and even *B. amaliae*, form an unresolved polytomy with this clade. In addition, species presently assigned to *Hirtomurex* and *Latiaxis* live in a deep water habitat, representing possible additional deep-water colonization/radiation events within Coralliophilinae.

Considering the global pattern of bathymetric distribution (~75% of known coralliophiline species in deep waters), a likely hypothesis for the coralliophiline radiation involves multiple colonizations of deep-water habitats, with many or most resulting in adaptive radiations. Unfortunately, the very limited information on the host associations of deep water Coralliophilinae (e.g., Taviani et al., 2009) is an impediment to a clear understanding of the factors involved in such radiations.

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LITERATURE CITED

- Felsenstein, J. 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution* 17: 368–376.
- Gohar, H.A.F. and G.N. Soliman. 1963. On the biology of three coralliophilids boring in living corals. *Publications of the Marine Biological Station, Al Ghardaqa, Red Sea*, 12: 99–126.
- Hillis, D.M. and C. Moritz, C. (eds.) 1990. *Molecular Systematics*. Sinauer, Sunderland, 588 pp.
- Jobb, G. 2007. Treefinder. June 2007 Version. Munich, Germany. Distributed by the author at <http://www.treefinder.de>.
- Kantor, Yu. I. 1995. On the morphology of the digestive system of *Latiaxis* (*Babelomurex*) (Gastropoda, Coralliophilidae) with notes on the phylogeny of the family. *Ruthenica* 5: 9–15.
- Kumar, S., K. Tamura, and M. Nei. 2004. MEGA3: Integrated software for Molecular Evolutionary Genetics Analysis and sequence alignment. *Briefings in Bioinformatics* 5: 150–163.
- Larget, B. and D.L. Simon. 1999. Markov Chain Monte Carlo Algorithms for the Bayesian Analysis of Phylogenetic Trees. *Molecular Biology and Evolution* 16: 750–759.
- Mariottini, P., C. Smriglio, and E. Rolán. 2005. *Coralliophila trigoi* (Gastropoda: Muricidae), a new species from the northeastern Atlantic Ocean. *The Nautilus* 119: 109–115.
- Marshall, B.A. and M. Oliverio. In press. The Recent Coralliophilinae of the New Zealand region, with descriptions of two new species (Gastropoda: Neogastropoda: Muricidae). *Molluscan Research*.
- Massin, C. 1987. *Reliquiacea*, a new genus of Coralliophilidae (Mollusca, Gastropoda). *Bulletin de l'Institut Royal de Sciences Naturelles de Belgique*, 57: 79–90.
- Massin, C. 1990. Biologie et ecologie de *Leptoconchus peronii* (Lamarck, 1818) (Gastropoda, Coralliophilidae) recoltée en Papouasie Nouvelle-Guinée, avec une redescription de l'espèce. *Bulletin de l'Institut Royal de Sciences Naturelles de Belgique* 60: 23–33.
- Nichols, S.A. 2005. An evaluation of support for older-level monophyly and interpretationship within the class Demospongiae using partial data from the large subunit rDNA and cytochrome oxidase subunit I. *Molecular Phylogenetics and Evolution* 34: 81–96.
- Nylander, J.A.A. 2004. MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
- Oliverio, M. 2008a. Coralliophilinae (Neogastropoda: Muricidae) from the southwest Pacific. In: Héros, V., R.H. Cowie, and P. Bouchet (eds.), *Tropical Deep-Sea Benthos* 25. *Mémoires du Muséum national d'Histoire naturelle* 196: 481–585.
- Oliverio, M. 2008b. Coralliophilinae (Neogastropoda: Muricidae) from the Marquesas Islands. *Journal of Conchology* 39: 569–584.
- Oliverio, M. In press. Coralliophiline diversity at Austral Islands (Neogastropoda: Muricidae). *Zoosystema*.
- Oliverio, M., M. Cervelli, and P. Mariottini. 2002. ITS2 rRNA evolution and its congruence with the phylogeny of muricid neogastropods (Caenogastropoda, Muricoidea). *Molecular Phylogenetics and Evolution* 25: 63–69.
- Oliverio, M. and P. Mariottini. 2001. A molecular framework for the phylogeny of *Coralliophila* and related muricoids. *Journal of Molluscan Studies* 67: 215–224.
- Philippe, H., U. Sörhannus, A. Baroin, R. Perasso, F. Gasse, and A. Adoutte. 1994. Comparison of molecular and paleontological data in diatoms suggests a major gap in the fossil record. *Journal of Evolutionary Biology* 7: 247–265.

- Ponder, W.F. 1974. The origin and evolution of the Neogastropoda. *Malacologia* 12: 295–338.
- Posada, D. and K.A. Crandall. 1998. Modeltest: testing the mode of DNA substitution. *Bioinformatics* 14: 817–818.
- Richter, A. and A.A. Luque. 2002. Current knowledge on Coralliophilidae (Gastropoda) and phylogenetic implication of anatomical and reproductive characters. (In:) Oliverio, M. and R. Chemello (eds.) *Systematics, Phylogeny and Biology of the Neogastropoda*. *Bollettino Malacologico, Supplemento* 4: 5–18.
- Ronquist, F. and J.P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
- Strimmer, K. and A. Rambaut. 2002. Inferring confidence sets of possibly misspecified gene trees. *Proceedings of the Royal Society Part B*, 269: 137–142.
- Swofford, D.L. 2002. PAUP*. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*, Version 4b10. Sinauer Associates, Sunderland, Massachusetts.
- Taviani, M., L. Angeletti, M. Dimech, C. Mifsud, A. Freiwald, M. G. Harasewych, and M. Oliverio. 2009. Coralliophilinae (Mollusca: Gastropoda) associated with deep-water coral banks in the Mediterranean. *The Nautilus* 123: 106–112.
- Thiele, J. 1929. *Handbuch der Systematischen Weichtierkunde* 1 (1). G. Fischer, Jena, 376 pp.
- Thompson, J.D., T.J. Gibson, F. Plewniak, F. Jeanmougin, and D.G. Higgins. 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, 25: 4876–4882.
- Ward, J. 1965. The digestive tract and its relation to feeding habits in the stenoglossan prosobranch *Coralliophila abbreviata* (Lamarck). *Canadian Journal of Zoology* 43: 447–464.
- Yang, Z. and B. Rannala. 1997. Bayesian phylogenetic inference using DNA sequences: a Markov chain Monte Carlo method. *Molecular Biology and Evolution*, 14: 717–724.